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Investigation in the laboratory of mucous trail detection in the terrestrial pulmonate snail *Mesodon thyroidus* (Say, 1817) (Mollusca: Gastropoda: Polygyridae)*

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Abstract: Many gastropods, including limpets, periwinkles, and mud snails, detect and follow mucous trails. The stylommatophoran pulmonate snail *Mesodon thyroidus* follow conspecific trails in the field, potentially following in the direction they were laid, as has been demonstrated for other pulmonates. This study investigated whether individuals of *M. thyroidus* directionally follows conspecific trails, and whether substrate type or incline influences trail following. Trail following was quantified on plexiglas and glass surfaces at horizontal, vertical, and 45° inclines. On horizontal plexiglas surfaces, 36% of *M. thyroidus* followed a marker trail made by a conspecific (n = 11). On horizontal glass surfaces, 45% of the snails followed a marker trail (n = 20). On glass (all inclines combined) 75% of snails that followed a conspecific trail followed it in the same direction it was laid (n = 60). On plexiglas (all inclines combined) 86% of trail-following proceeded in the direction the trail was laid (n = 33). The difference in the results across the two substrates could indicate a behavioral reaction to the chemical difference of the substrates. Preliminary observations of tentacle movements and of the mucous trails indicate that previously laid trails can be detected before the foot of the following snail contacts the marker trail.

Key words: trail following, mucus, chemoreception, behavior

Moving snails leave mucous trails that can be detected by other organisms, including other snails. Many snails can detect or follow mucous trails of conspecifics and non-conspecifics (Cook 2001). Mucous trail following is used in homing, finding food sources and mates, and forming aggregations (Chase 1986, Tankersley 1989, Cook 2001). Gastropods often move faster on previously-laid mucous trails than on bare substrate (Wareing 1986, Erlandsson and Kostylev 1995) and can detect and respond to the trail's age as well as the physiological state of the individual that left it, avoiding trails left by stressed individuals (Edwards and Davies 2002). Understanding this behavior in gastropods could assist with conservation of endangered species and control of invasive species.

Most pulmonate gastropods have two pairs of tentacles that are used in chemoreception and to follow mucous trails (Chase 1986, Lemaire and Chase 1998). Both the oral (anterior) and optic (posterior) tentacles may be used when following mucous trails, and to detect odors associated with the trail (Chase 1986, Stirling and Hamilton 1986). Chase and Croll (1981) found that the giant African land snail *Achatina fulica* Bowdich, 1822 primarily uses its oral tentacles for following substrate-bound mucus, while the optic tentacles are used for tracking airborne odors. While tracking airborne odors, snails have been observed to hold their optic tentacles at a characteristic angle, around 90° in the horizontal plane with respect to each other (Lemaire and Chase 1998, Davis 2004), which may allow the snail to compare information from its right side to its left side. This tentacle position may also facilitate trail-following. Trails contain information that can be detected by chemosensory and mechanosensory receptors (Denny 1989). Trail-following may be a primary mechanism to find mates, given that most terrestrial pulmonates cannot self-fertilize despite being hermaphroditic (Stanisic 1998).

Mesodon thyroidus (Say, 1817) is a species of terrestrial snail native to the eastern United States (Burch 1962, Hubricht 1985) and is common in Lawrence, Kansas, U.S.A. (Pilsbry 1940, Leonard 1959). It eats plants and fungus (Burch 1962) and, in Kansas, is often found in large groups (> 100 individuals in 1 m^2). Pearce (1990) showed that individuals of *M. thyroidus* follow conspecifics by marking the paths of snails in the field (using the "spool and line" technique), but did not examine mucous trails or the role of trail-following.

To follow up on Pearce's (1990) study I asked how often individuals of *Mesodon thyroidus* follow conspecific trails and if they can follow in the direction that the trail was laid. I quantified trail-following on two different substrates (plexiglas and glass) at three different inclines (horizontal, vertical, and 45°). Snails encounter many inclines in their natural environment, and I expected that substrate incline would not influence trail-following. However, snails often crawl in straight lines up vertical surfaces, which could

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change the tortuosity (or curviness) of the trail by incline. I also explored the effects of trail remnants on trail following because plexiglas and glass plates retain mucus differentially after cleaning. The goals of this study were to determine: (1) how often the polygyrid snails of *Mesodon thyroidus* follow mucous trails made by conspecifics, (2) if the substrate incline (horizontal, 45°, and vertical) affects trail following, and (3) the effects of trail remnants on trail following.

METHODS

Approximately 100 specimens of *Mesodon thyroidus* collected from a compost pile in Lawrence, Kansas, U.S.A., were brought into the laboratory. Sexually mature snails (n = 26), determined by the presence of a lip on the aperture, were kept for at least 7 days in individual boxes with damp paper towels (for moisture), and a container of moist peat moss at least 2 cm deep to provide a substrate for egg-laying. Snails were kept at room temperature (20°C) and in natural light near windows in the laboratory, and were fed carrots or lettuce on alternate days. All snails used in this experiment can be found at the University of Kansas Natural History Museum, catalog numbers 002437-002462.

To test whether a snail could detect a conspecific mucous trail, the first snail—designated the "marker" snail—was allowed to crawl on a 20 cm × 20 cm pane of picture glass. In each trial a marker snail was centered at an edge of the pane of glass facing the center and allowed to crawl until it reached an edge. Trials were stopped if a snail did not move for more than 5 min or if the mucous trail was not straight for at least one body length. After the snail reached the edge of the glass it was removed. The glass was then rotated 90° (randomized between clockwise and counter-clockwise) and a second (experimental) snail was placed at least one body length from the trail at approximately 90° to the marker trail. The experimental snail was allowed to crawl until it reached the edge of the glass or was removed due to lack of movement; the trial was discarded if the snail did not move for at least 5 min. Trials were conducted on horizontal, sloped (45° from the horizontal), and vertical panes to test if the incline of the substrate affected trail following (both marker and experimental snails crawled on panes at the same incline). All trials were videotaped to facilitate observation of tentacle movements, their angle, and to confirm the paths of the snails. After the experimental snail was removed, the mucus was allowed to dry on the glass before being stained (see below). To ensure independent trials, each pair of marker and experimental snails was used only once. Individual shells were numbered with a paint pen.

The trails were stained by soaking the glass panes for 1-5 min in a suspension of carbon particles (laser printer toner) in distilled water (Karowe *et al.* 1993). These stained trails were photocopied for record keeping. Afterward, the glass plates were soaked for 5 min in 5% acetic acid, washed with soap and distilled water, rinsed with distilled water, soaked for 20 min in 3% sodium hypochlorite, and rinsed six times with distilled water. This cleaning process removed all traces of the mucus from the glass, as confirmed by exposure to carbon particles.

To test for the effects of trail remnants on trail following, plexiglas substrates were used. For plexiglas substrates (20 cm × 20 cm), the procedure was similar to that used with glass, with two exceptions. Snails were kept in groups in containers rather than individually, and each group of snails was tested against another group. Second, the plexiglas was washed with soap and distilled water, rinsed with distilled water, and then rinsed with 95% ethanol. The porous plexi-

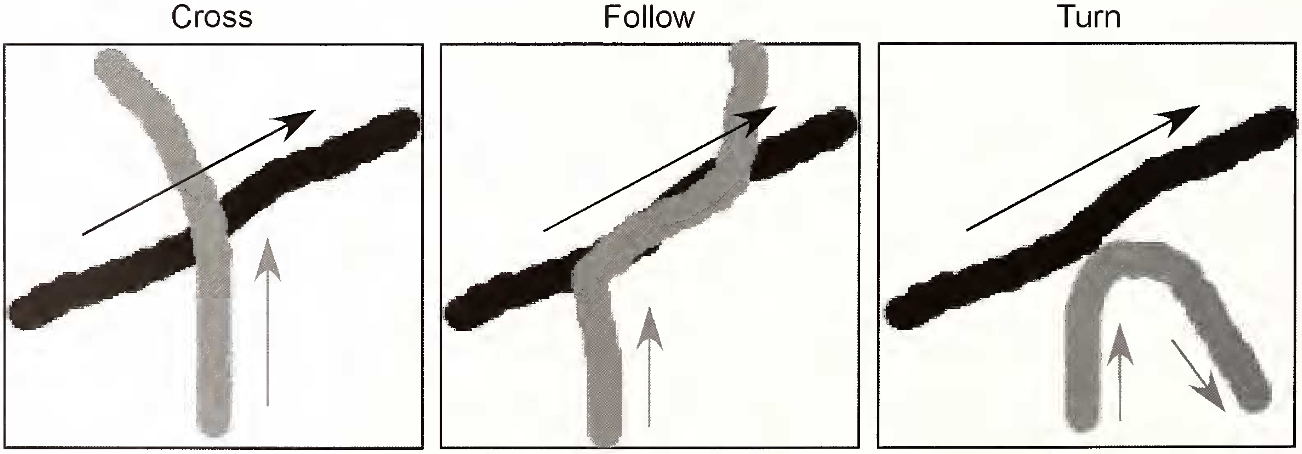

Figure 1. Categories used to score snail behavior; marker (first) trail is black, experimental (second) trail is gray.

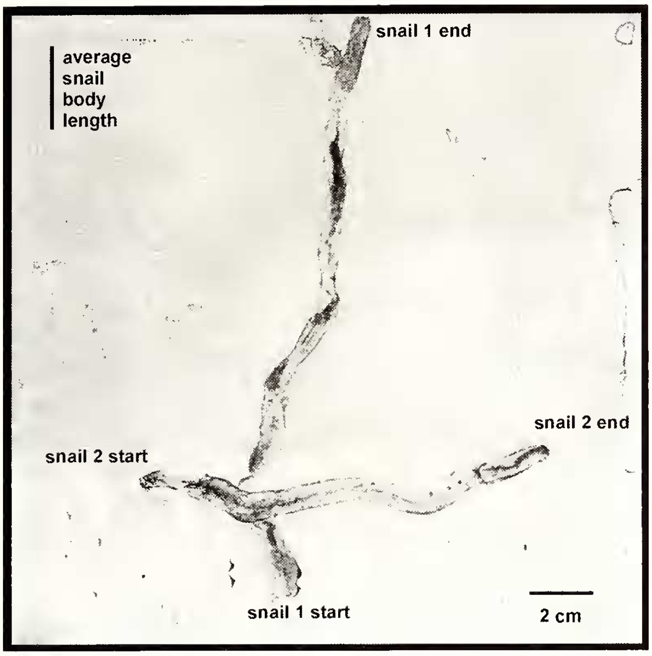

Figure 2. Example of stained trails showing a cross response.

glas substrate retained portions of previous trails. Thus, experimental snails on plexiglas were tested in the presence of remnant trails as well as a marker trail. The presence of remnant trails was confirmed by staining with carbon particles after these trials were conducted. Some of these trials were traced onto acetate sheets after being stained with colored chalk before the carbon particle method was perfected. All other procedures were the same.

For glass and plexiglas substrates, the behavior of each experimental snail was analyzed by examining its mucous trail. I characterized each trial as belonging in one of three categories: cross, follow, and turn (Fig. 1). A cross was defined as any overlap by an experimental trail of less than one body length of a marker snail trail (Fig. 2). A follow was defined as an overlap of at least one body length of marker and experimental trails (Fig. 3). A turn was defined as a complete turn (180° ± 15°) of an experimental trail occurring just before or adjacent to a marker trail (Fig. 4). Both turning and following were considered to be responses because the snail appeared to have an obvious behavioral response to a marker snail's trail. Although crossing a trail was considered a non-response behavior, it does not imply that the snail did not detect the trail.

To quantify how often individuals of *Mesodon thyroidus* follow mucous trails, the counts of the behavioral results of trail encounters were compared by category to two null models. These results were also used to test for a difference by substrate incline. Fisher's exact test (Sokal and Rohlf 1995) was used to test the grouped results of response (turn/follow) and non-response (cross) categories against the null models. Because of low counts the results were grouped as response (turn/follow) and non-response (cross) rather than as the three scored categories. The first null model, which was used on both plexiglas and glass trials, was generated by scoring trails against randomly drawn straight lines rather than against the marker trails. These lines were drawn between two randomly chosen points along the edges of a grid that was size-matched to the substrates. The lines were then scored against an experimental snail's path to generate expected responses for a "null" trail. I used these scores as the

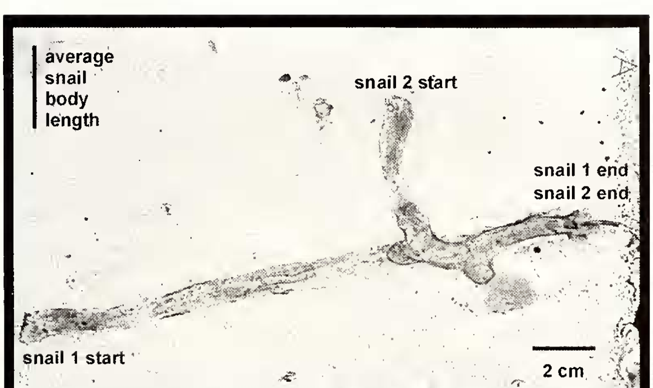

Figure 3. Example of stained trails showing a follow response.

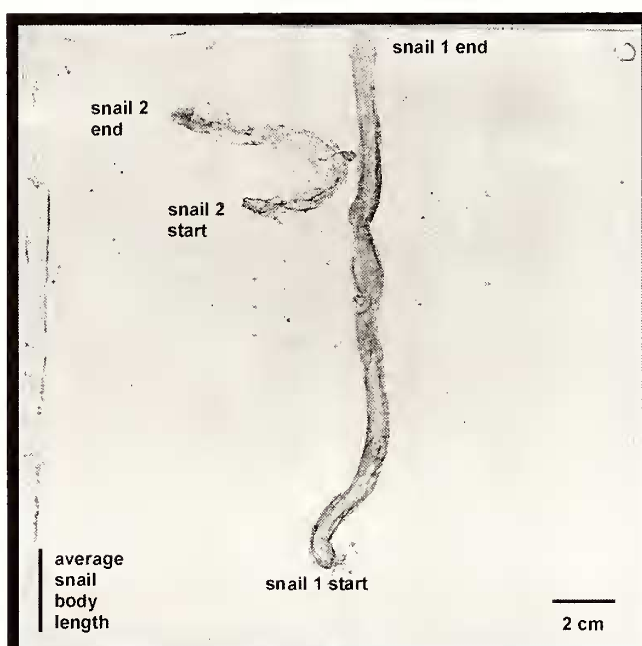

Figure 4. Example of stained trails showing a turn response.

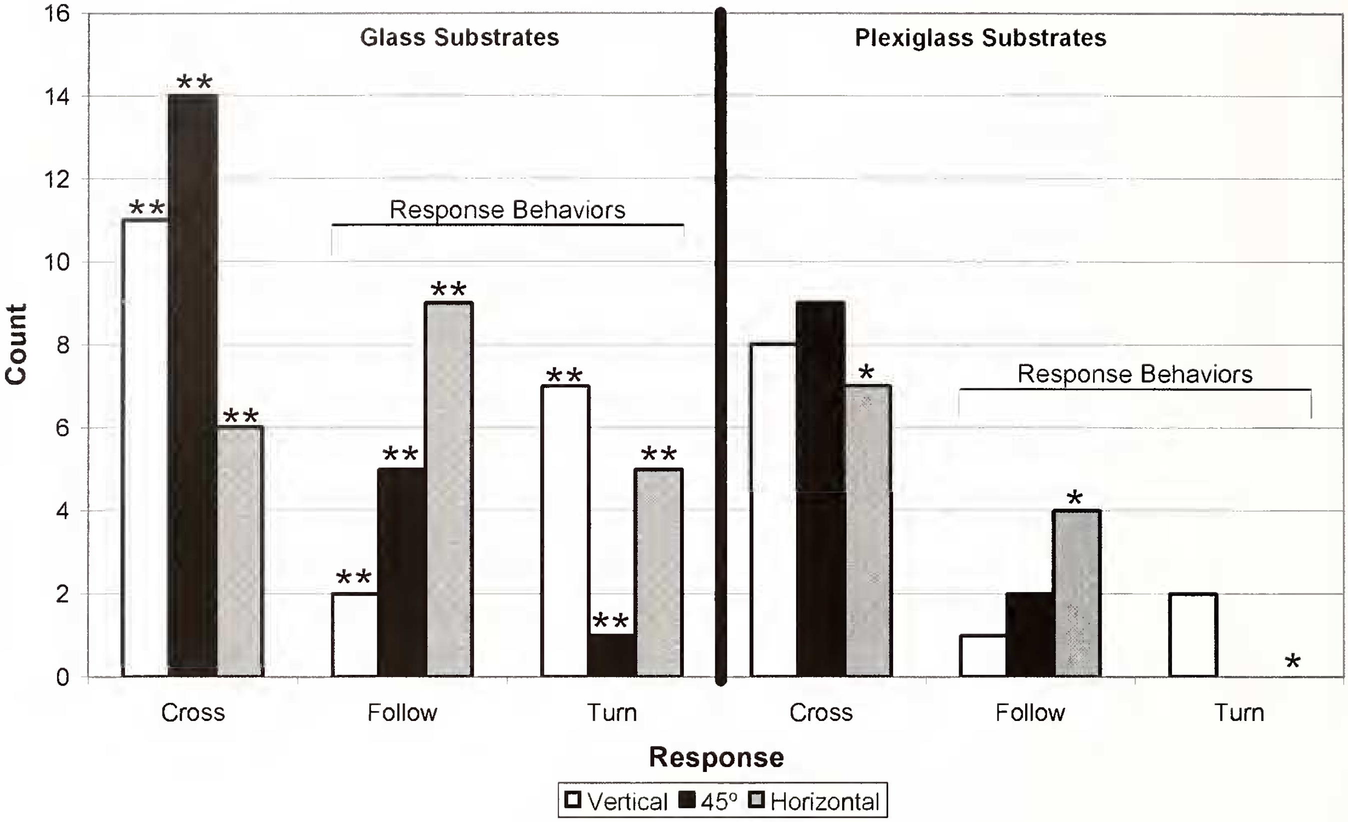

Figure 5. Response of experimental snail to marker trail on glass and plexiglas substrates. On both substrates, snails were able to detect trails at all substrate inclines and followed most often on horizontal surfaces. * = Results by incline are significantly different than the straight line null ($\alpha = 0.05$) with straight line nulls. ** = Results by incline are significantly different than the straight line null ($\alpha = 0.05$) with both "marker" trail and straight line nulls.

expected values in Fisher's exact test. The second null model used on both plexiglas and glass trials quantified trail crossing, following, and turning for two overlaid marker trails, selected randomly. These trails were overlapped by randomly orienting the "null" marker substrate (0°, 90°, 180°, and 270° from its original orientation) and then lining up the corners of the substrates between the two trials. The two marker trails were then scored. The results from the second null model generated an additional set of expected values. These expected results were tested using the same statistics as the "null lines." The second null model did not work as well for the plexiglas substrate because many trials were recorded on acetate sheets that did not include information on snail orientation or trail location on the substrate. This meant that not all plexiglas trials could be tested the same way. These problems make the second null model much less reliable for the plexiglas substrate than the straight line null model. However, both models show the same trend with the results.

To analyze the path of the snail trails, I wrote a program in Visual Basic for Applications (VBA—Microsoft) in Excel (Microsoft) to calculate the length, tortuosity, and angle of approach of the tracker snail to the marker path (Davis 2005). Paths were digitized using Didger (v. 2, Golden Software, Inc.) and uploaded into the VBA program as two-dimensional points. The total length of the path was calculated by adding successive line segments. Tortuosity, a measure of the curviness of the trail, was calculated by taking the ratio of the total length of the path of the snail to the straight line distance between the first and last points (start and stop points of the trail). High tortuosity in the marker trail could hamper the experimental snail's trail-following ability. A general linear model (GLM) was used to test the tortuosity ratio (beginning-to-end distance/total distance) against both incline of substrate (vertical, horizontal, 45°) and behavioral response (cross, follow, turn). GLM was also used to test behavioral response of the snail against tortuosity (Sokal and Rohlf 1995). The angle between paths was determined by calculating the angle of approach of the experimental snail in relation to the marker snail. These angles were divided into two groups—those that were within 45° of

Table 1. Expected values for Fisher's exact tests generated from the two different null models.

Trials on glass (single trail)

Straight "Null" Lines	Cross	Follow	Turn	"Marker" trail as null	Cross	Follow	Turn
Incline				Incline			
Vertical	43	6	0	Vertical	56	2	0
Horizontal	41	5	2	Horizontal	57	3	1
45°	47	2	0	45°	63	4	3

Trials on plexiglas (most recent trail)

Straight "Null" Lines	Cross	Follow	Turn	"Marker" trail as null	Cross	Follow	Turn
Incline				Incline			
Vertical	39	2	0	Vertical	34	5	1
Horizontal	31	1	1	Horizontal	33	4	1
45°	48	2	0	45°	27	4	1

perpendicular to the marker trail and those that were within 45° of parallel to the marker trail. A G-test was used to determine if the angle of approach of the experimental trail was independent of the behavioral response of the experimental snail (Sokal and Rohlf 1995). In addition, I tested if the angle of approach between trails affected the directionality of following by using a Chi-squared test (a G-test could not be used because of counts of zero).

RESULTS

Individuals of *Mesodon thyroidus* were able to detect and follow trails on both substrates and at all inclines, but trail-following diminished as the inclination approached vertical (Fig. 5). At each inclination, snails followed more trails on glass than on plexiglas. On glass surfaces, snails responded to conspecific trails significantly more often than was predicted by either null model at all inclinations (Fisher's Exact Test, $\alpha = 0.05$, Tables 1 and 2), but differences between inclinations were significant (Fig. 5). An individual snail did not necessarily show the same response to every trail encountered. Of the snails that followed on glass surfaces, 75% of them followed in the direction in which the marker trail had been laid. On plexiglas substrates, the behavioral responses indicate that snails detected trails at all inclinations, even in the presence of remnant trails. However, responses to marker trails were statistically significant ($\alpha = 0.05$) for horizontal surfaces only (Table 2). Eighty-six percent of snails that followed a conspecific trail did so in the same direction in which the trail was laid. The plexiglas null model using superimposed marker trails was problematic because some of these trials were conducted before the carbon particle method was developed and the trails were traced without recording their orientation on the plexiglas.

Observations of optic tentacles showed that optic tentacles were often held parallel to the substrate and oral tentacles alternately touched the substrate while the snail was at rest and when it was moving. A snail was often seen lifting its head from the substrate and moving its head from side to side while its tentacles remained stationary with respect to the head.

On glass substrates, the results of the trail analysis (using the VBA program) indicated that there was not a significant difference between the tortuosity of the trail and the behavioral response (from GLM of tortuosity by behavioral response and snail order: Response [Cross, Follow, Turn]:

Table 2. Results of Fisher's exact test. * = results that are significantly different than the null ($\alpha = 0.05$), indicating that snails are responding to trails.

With straight line "trails" as null	Incline		
Probability	Vertical	45°	Horizontal
2-tailed, single trail (glass)	0.0076*	0.0059*	0.0002*
2-tailed, most recent trail (plexiglas)	0.0574	0.1455	0.0269*
With "marker" trail as null	**Incline**		
Probability	Vertical	45°	Horizontal
2-tailed, single trail (glass)	0.0004*	0.0355*	4.553×10^{-8}*
2-tailed, most recent trail (plexiglas)	0.3848	1.0	0.1785

F = 0.30, df = 2 p = 0.744, Snail Order: F = 0.73, df = 1 p = 0.395, Interaction [Snail Order*Response]: F=0.41, df = 2 p = 0.662). On plexiglas, there was a significant difference between the tortuosity of the trail and the behavioral response (from GLM of tortuosity by behavioral response and snail order: Response [Cross, Follow, Turn]: F = 11.26, df = 2 p = 0.0, Snail Order: F = 2.03, df = 1 p = 0.159, Interaction [Snail Order*Response]: F=3.66, df = 2 p = 0.032). A graphical representation of the tortuosity data from glass can be seen in Fig. 6. One trial (45° glass, cross), however, could not be digitized from the carbon visualization and so could not be included in the trail analysis using the VBA program. Similarly, on glass substrates, there was no significant correlation of angle difference (between marker and experimental snail) and behavioral response (cross, response) (G = 0.86, p = 0.35, df = 1) for the angle between the two trails. However, on plexiglas substrates there was a significant correlation of angle difference and behavioral response (G = 13.5, p < 0.005, df = 1). All but one of the follow responses on plexiglas occurred with an angle that was within 45° of parallel to the trail. With the subset of snails that followed on both substrates, there was no significant difference between the angle difference (between marker and experimental snail) and directionality of the follow response (right way, wrong way) (glass χ^2 = 0.042, p = 0.838, df = 1; plexiglas χ^2 = 0.194, p = 0.659, df = 1). Table 3 summarizes the results of the trail analysis.

DISCUSSION

Individuals of *Mesodon thyroidus* were able to detect conspecific mucous trails at all three substrate inclines tested in this study (horizontal, 45°, and vertical). The substrate type and incline had the greatest effects on the behavioral responses of the snails. The effect of incline is interesting given that snails encounter all inclines of substrate in their environment. Individuals of *M. thyroidus* did not respond to

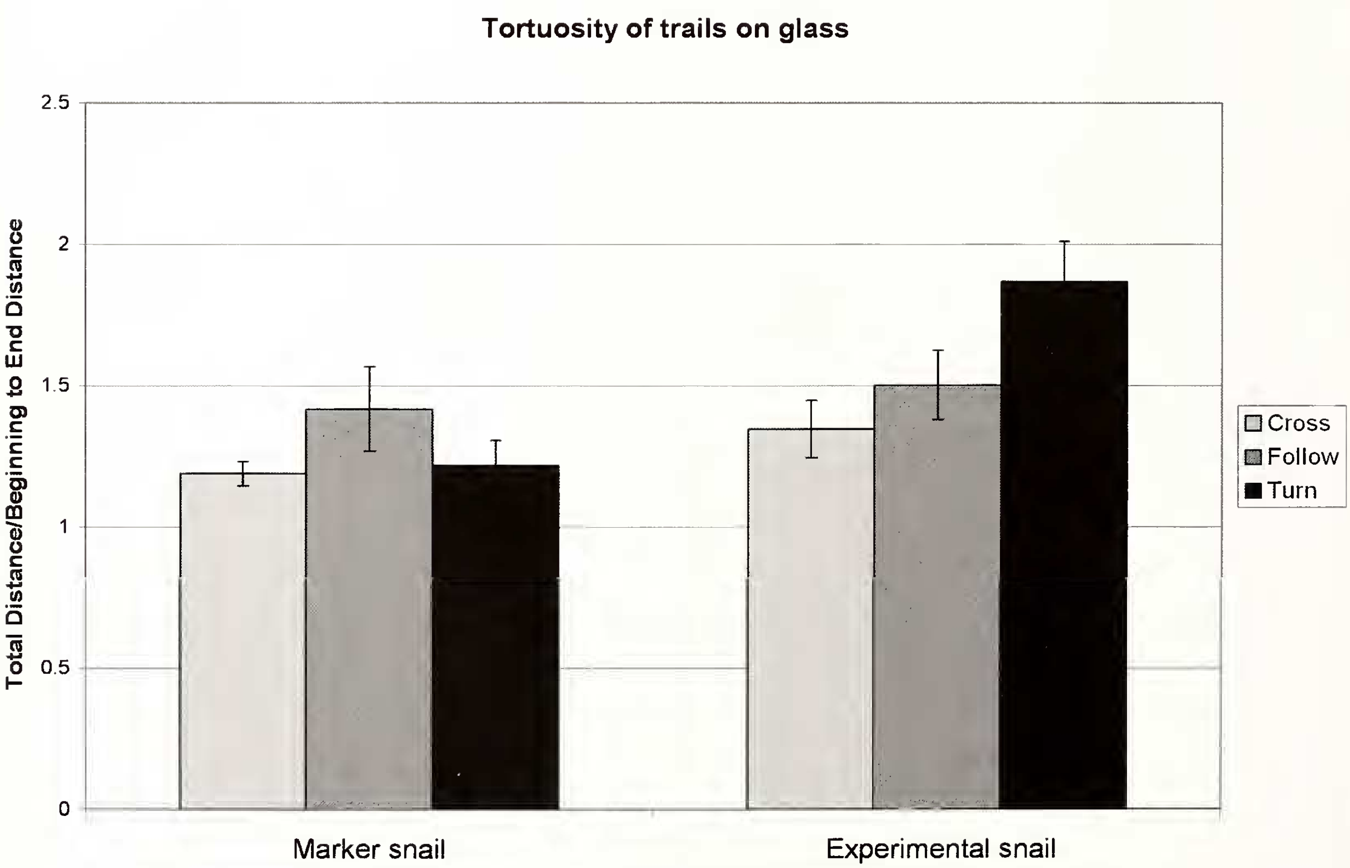

Figure 6. Results from VBA analysis of snail paths on glass substrates. One outlier data point (experimental cross) was excluded because the trail returned to the same place it started, causing the ratio of total distance/beginning to end distance to be very large. Error bars indicate plus/minus one standard error.

Table 3. Statistics on the results of quantitative analysis of trails using the VBA program. *, results that are significantly different than the null ($\alpha = 0.05$)

Statistical Test	Substrate	Results						
General Linear Model (GLM) of tortuosity of trail by behavioral response and snail order	Glass	Source	DF	Seq SS	Adj SS	Adj MS	F	P
		Response	2	22.61	22.61	11.30	0.30	0.744
		Snail	1	55.27	27.79	27.79	0.73	0.395
		Response*Snail	2	31.48	31.48	15.74	0.41	0.662
		Error	112	4262.97	4262.97	38.06		
		Total	117	4372.32				
	Plexiglas	Source	DF	Seq SS	Adj SS	Adj MS	F	P
		Response	2	34.682	34.682	17.341	11.26	0.000*
		Snail	1	0.217	3.134	3.134	2.03	0.159
		Response*Snail	2	11.276	11.276	5.638	3.66	0.032*
		Error	60	92.414	92.414	1.540		
		Total	65	138.588				
G-test of the angle difference by behavioral response (cross/follow)	Glass	$G = 0.86$, $p = 0.35$, df =1						
	Plexiglas	$G = 13.5$, $p < 0.005$*, df =1						
Chi-squared test of the angle difference by following direction	Glass	$\chi^2 = 0.042$, $p = 0.838$, df = 1						
	Plexiglas	$\chi^2 = 0.194$, $p = 0.659$, df = 1						

every trail encountered in this experiment, as indicated by the cross responses. On glass substrates (single mucous trail) no significant effect of inclination of substrate was seen on behavioral response. On plexiglas substrates (most recent mucous trail) only the horizontal incline showed statistically significant response behavior compared to the straight null lines (which were a better null for these data). Cain and Cowie (1978) found that snails with flatter-spired shells were more likely to be active on horizontal surfaces, which could explain why the horizontal incline showed statistically significant response behavior in both experiments. However, these snails are often found climbing trees in the southern part of their range (personal observations, Davis *et al.* 2004). The non-significance of the results on plexiglas could be due to the presence of remnant trails. But it could also be an artifact of the small counts due to sample size (n = 11 for each incline) or a difference in chemical composition of the substrate. I did not observe that snails had any potential difficulties in climbing on plexiglas or any other behavioral reaction to indicate a difference on plexiglas versus glass. The results on plexiglas were important in demonstrating that *M. thyroidus* can detect the most recent mucous trail when remnant trails exist in the environment. Staining of plexiglas showed physical evidence of remnant trails, which may or may not have been detected. Unfortunately, the presence of remnant trails on what was believed to be "clean" plexiglas was only confirmed by staining with carbon particles after this experiment was conducted. However, these results can be used as preliminary data on the effect of trail remnants on trail following. As expected, this experiment verified the field experiments of Pearce (1990), in which many mucous trails were present in the environment and conspecific following was observed.

The mechanisms used by snails to detect trails are not well understood (Stirling and Hamilton 1986, Denny 1989, Erlandsson and Kostylev 1995) but the turn response I observed indicates that trails can be detected before the foot of the following snail contacts the marker snail's trail. The tentacles of snails can be used to track odors by both tropotaxis and anemotaxis (Chase and Croll 1981, Lemaire and Chase 1998). In the terrestrial pulmonate *Achatina fulica*, Chase and Croll (1981) observed that both pairs of tentacles are used to orient to concentration gradients and to mucous trails. I was able to confirm Chase and Croll's (1981) observation that both pairs of tentacles were moved and seemed to be used when following trails. It is possible that each snail could detect every trail it encountered in the experiment but responded only to some of them, which is why I observed many more cross responses than follow or turn responses.

In this study, there were clear differences between the behavioral results obtained across the two tested substrates. All of the snails tested against the glass substrate were individually housed. However, the snails tested on plexiglas were kept in group containers, and it is possible that recent mating of the marker snail could be assessed through the mucous trail and effected the response behavior of the experimental snail. Feeding time was consistent across all snails. Other studies with non-pulmonate snails have shown that the physiological state of the individual, such as stress due to starvation, can be assessed (Edwards and Davies 2002) by a following snail. I do not think that food-stress was a factor in my results.

If we understand the mechanisms that are used to detect and follow trails in pulmonate snails then it is possible that we can use this knowledge to aid in conservation. For example, the carnivorous pulmonate snail *Euglandina rosea* (Férussac, 1821) uses mucous trails to find its prey (Cook 1985, Davis 2005) and has been implicated in the decline and extinction of many native snails on the islands of Hawaii, Tahiti, and Moorea among others (Cowie and Robinson 2003). Understanding the mechanisms of trail detection could be used to create false trails leading to traps, controlling the pest species, if we can assume that those mucous trails are followed in the direction that they were laid.

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